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Reproductive status and testosterone among females in cooperative mole-rat societies

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ABSTRACT

Sexual selection acts on traits that increase reproductive success. Variation in reproductive success is often higher among males than females. Consequently, sexual selection has been studied extensively in males while its possible role in females has only recently attracted considerable attention. In some cooperatively breeding species females compete intensely for reproductive opportunities and may thereby have evolved 'male-like' traits such as increased intra-sexual aggression and exaggerated secondary sexual traits. The expression of the latter tends to be testosterone-dependent in male vertebrates but whether this is also the case among females remains poorly understood. Here, we compare two cooperatively breeding mole-rat species (Natal, *Cryptomys hottentotus natalensis*, and Damaraland mole-rats, *Fukomys damarensis*) in which a single female monopolises reproduction through behavioural and physiological suppression, respectively, to evaluate the effect of female intra-sexual competition. Consistent with the hypothesis that intra-sexual competition has shaped patterns of testosterone (T) secretion among females in these species, we show that (i) female T levels in both species are significantly higher among breeding (BFs) (who may face the highest degree of intra-sexual competition) compared to non-breeding females (NBFs), (ii) that T levels in both species are significantly higher when access to unrelated males can be assumed to be greatest (i.e., wet season), and (iii) that the average female T levels are a full order of magnitude higher in the absence of a physiological mechanism of reproductive suppression. Together, our results suggest a role for intra-sexual competition in shaping patterns of T secretion among females of the social mole-rats and raise the possibility of a modulatory role for the mode of reproductive suppression on competition-related traits in females.

1. Introduction

Sexual selection acts on traits that affect the reproductive success of an individual and is thought to have led to elaborate traits such as increased body size or ornaments observed in males of many species (Anderson, 1994). The conspicuousness of such traits among males may account for the marked sex bias in studies of sexual selection (Clutton-Brock, 2007, 2009). Accordingly, studies on sexual selection in females often focus on species where females exhibit pronounced sexual secondary characters such as in species with reversed sex roles (Kvarnemo et al., 2007; Kvarnemo and Simmons, 1999; Langmore et al., 2002). The comparative lack of studies of sexual selection in females can partly be attributed to the common assumption that females exhibit less variation in reproductive success and should thus be less affected by sexual selection (Hauber and Lacey, 2005; Reeve and Pfennig, 2003). However, females may compete intensely for mates in species without sex-role reversal and may exhibit a number of traits commonly associated with males, such as high intra-sexual aggression, sexual displays and elevated testosterone levels (Clutton-Brock et al., 2006; Langmore et al., 2002), suggesting that the role of sexual selection among females warrants closer attention (Clutton-Brock, 2007, 2009). Recent work has shown that variance in female reproductive success can be very high in social vertebrates, particularly in cooperative breeders with high reproductive skew (in which a small number of females monopolize the majority of reproduction) (Clutton-Brock, 2009; Hauber and Lacey, 2005). Indeed, in a number of cooperatively breeding vertebrates marked intra-sexual aggression among females is common, particularly in a reproductive context (Clarke and Faulkes, 1997; Clutton-Brock et al., 2006; Cooney and Bennett, 2000; Desjardins et al., 2008b; Kutsukake and Clutton-Brock, 2005). In addition, body mass or size is a key determinant in acquiring and/or maintaining a breeding position in females of various cooperatively breeding species (Faulkes and Abbott, 1997; Heg et al., 2004; Hodge et al., 2008). Accordingly, the degree of sexual dimorphism in traits used in intra-sexual competition appears to be reduced in some cooperatively breeding

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species (Rubenstein and Lovette, 2009). Thus, cooperatively breeding species may be particularly suitable to evaluate the effects of sexual selection on females.

In male vertebrates the expression of traits that enhance access to mates such as aggression, large body size and elaborate sexual signals is often mediated by the androgen testosterone (T) (Clutton-Brock, 1988; Hau, 2007; Wingfield et al., 1990). Male T levels frequently vary with social and environmental stimuli and tend to be elevated during breeding periods and in response to intrasexual encounters or social instability (captured in the challenge hypothesis) (Goymann, 2009; Wingfield et al., 1990). The challenge hypothesis has found support in males across vertebrate taxa (Hirschenhauser and Oliveira, 2006). In contrast, the possible role of environmental and social stimuli on patterns of T in females has been largely neglected (Moore, 2007). Evidence suggests that the expression of morphological and behavioural traits linked to intra-sexual competition in females can be affected by T similar to males (Staub and de Beer, 1997). In addition, female T levels may vary seasonally and in response to social interactions (Beehner et al., 2005; Calisi and Hews, 2007; Desjardins et al., 2006; Langmore et al., 2002; Sandell, 2007). Despite the potential significance of T in competition among females, T is still considered to be of relatively minor importance in females and few studies have explored the effects of intra-sexual competition on circulating T levels in female vertebrates (Staub and de Beer, 1997).

In the current study we investigated the extent to which intrasexual competition may have shaped the patterns of T secretion among females in cooperatively breeding mole-rat societies. Social mole-rats offer a novel opportunity for studies of this kind as, while all species show high reproductive skew (only one female breeder per colony), closely-related species can differ markedly in the extent to which this skew arises from behavioural mechanisms (i.e., intra-sexual aggression) alone (Faulkes and Bennett, 2009). Reproductive suppression in mole-rats is thought to result from a combination of control by the breeding female (BF) or queen (e.g. aggression) and self-restraint in non-breeding females (NBFs) due to a lack of unrelated males (Faulkes and Bennett, 2009). Mole-rats exploit the subterranean niche and since the digging required for breeding dispersal is much less energetically costly in soft soils, access to unrelated males is assumed to be linked to rainfall patterns and consequently, the dispersal increases strongly with precipitation (Bishop and Jarvis, 2004; Burland et al., 2004; Faulkes and Bennett, 2009). When new breeding opportunities arise, escalated aggression among females that can result in the death of competitors has been observed in several mole-rat species (Cooney and Bennett, 2000; Faulkes and Abbott, 1997; Margulis et al., 1995). Here we exploit the variation in modes of reproductive suppression among two social mole-rat species to investigate not only how intra-sexual competition has shaped T levels among females in high skew species, but to consider the possibility that the strength of selection on androgen levels in such species may depend upon the mechanisms through which intra-sexual reproductive conflict is resolved. Where intrasexual reproductive competition is resolved solely through behavioural means (i.e., NBFs show comparable reproductive physiology to BFs), selection may differentially favour the elevation of circulating T levels to promote those traits that may favour success in competition (e.g. aggression). Specifically, we compare and contrast the patterns of circulating T among females in two closely related mole-rat species that differ in their modes of suppression (the Natal mole-rat, *Cryptomys hottentotus natalensis*, and the Damaraland mole-rat, *Fukomys damarensis*, Table 1). While both species live in colonies in which a single female monopolizes reproduction, in Natal mole-rats NBFs are physiologically capable of breeding (Oosthuizen et al., 2008) whereas in Damaraland mole-rats NBFs experience a block to ovulation attributable to the down-regulation of the pituitary sensitivity to gonadotropin releasing hormone (GnRH) (Bennett et al., 1996; Molteno and Bennett, 2002). This may be linked to the variation in ecological constraints to dispersal and hence breeding opportunities (i.e., unrelated males entering a colony or NBFs leaving their natal colony) that both species experience as Natal mole-rats occur in more mesic habitats than Damaraland mole-rats (Faulkes and Bennett, 2009). Consequently, while sexual selection may have favoured 'androgenised' aggressive females in both species (Cooney and Bennett, 2000; Faulkes and Abbott, 1997), selection for androgen-mediated traits may be substantially stronger in Natal mole-rat societies as intra-sexual traits could be the principal means through which their reproductive monopolies are maintained. We therefore tested (i) whether Natal mole-rat females exhibit higher T levels than Damaraland mole-rat females. Both species breed throughout the year, nevertheless, NBFs of both species exhibit an up-regulation of their pituitary in response to rainfall; the baseline and response levels of luteinizing hormone (LH) and pituitary sensitivity are elevated during this period in Natal and Damaraland mole-rats, respectively (Oosthuizen et al., 2008; Young et al., 2010). Our second aim was therefore to test (ii) whether circulating T levels would be elevated during the wet season, when NBFs may have access to reproductive opportunities and hence, challenges to the breeding monopoly of the BF are likely to occur. Lastly, we predicted that (iii) BFs would exhibit higher T levels than NBFs as a result of the intra-sexual challenges to their breeding monopoly that they may experience by NBFs. We also tested whether this is correlated with body mass as a proxy for age or linked with breeding status irrespective of size.

Table 1
Key life-history, environmental and physiological traits of Natal and Damaraland mole-rats.

	Natal mole-rat	Damaraland mole-rat
Reproductive skew	1 Breeding female	1 Breeding female
Group size	8.8 ± 3.7	8.2 ± 4.8
Habitat	Mesic	Arid
Mode of suppression	Behavioural	Physiological
Reproduction	Aseasonal	Aseasonal
HPG-axis in NBFs	Seasonal upregulation	Seasonal upregulation

HPG: hypothalamic-pituitary-gonadal, NBF: non-breeding female.

2. Material and methods

2.1. Study sites and trapping methods

We caught Natal mole-rats on a bimonthly basis from March 2003 to January 2004 and in March and July 2006 on a golf course surrounded by montane grassland at Glengarry Park (1500 m altitude) in the Kamberg region of KwaZulu-Natal (25°58'S; 21°49'E). Damaraland mole-rats were trapped at the Tswalu Kalahari Reserve in the southern Kalahari (27°13'S, 22°28'E) during March and October 2004 and March 2005. Captures conducted from May to October coincided with the dry season in both locations while the remainder of the year received the majority of precipitation and was thus defined as the wet season (Young et al., 2010). In both locations captures were conducted by exposing mole-rat tunnels close or underneath fresh molehills and setting modified Hickman life-traps baited with sweet potato at the entrances of those tunnels. All animals were live-trapped. Colony members were housed together in plastic containers until the entire colony had been captured. They were provided with wood shavings or soil as nesting and were fed on sweet potato. Group sizes were similar for both species (Natal mole-rats: 8.8 ± 3.7 individuals, $n = 22$ colonies, Damaraland mole-rats: 8.2 ± 4.8 individuals, $n = 17$